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On the Anatomy and Development of Echinococcus veterinorum. By Thomas Huxley, F.R.S.

[With a Plate.]

On the 25th of November, 1852, a fine female Zebra, whilst at play within its paddock, accidentally broke its neck. The animal had always appeared to be quite healthy, and it was in perfectly good condition—but, upon examination, its liver was found to be one mass of cysts, varying in size from a child's head downwards. The liver was taken out of the body on the day succeeding the animal's death* —and on the 27th I proceeded to examine the contents of one of the largest cysts (with a portion of its wall) and one of the smaller cysts.

It was at once obvious that the cysts contained the *Echinococcus veterinorum*; and I may here mention that the *Echinococci* were in full life, and remained so for three days, until, in fact, the fluid in which they were contained had become slightly offensive.

It will conduce to clearness perhaps, if I state in successive order I. What I saw myself. II. The theory of the formation of the *Echinococcus*-cysts, and of their relation to other forms of Entozoa, which I have to offer. III. What has been done hitherto.

I. The cysts are nearly spherical vesicles having a very elastic proper wall; so elastic, in fact, as to exercise a continual tension upon the contained fluid, which, if the cyst be pierced, spurts out in a jet, for some time.

The outermost layer of the cyst is an adventitious membrane, formed by the infested animal around the *Echinococcus*-cyst, as it would be developed round any other foreign body; with this I have nothing to do. Within this, and in nowise adherent to it, follows the proper wall of the *Echinococcus*-cyst, which must be carefully distinguished into two portions. The outer is thick, yellowish and constituted by a great number of delicate, structureless laminæ composed of a substance closely resembling chitine. It is to this laminated membrane that the elasticity of the cysts is due—and it must be regarded as precisely analogous to those structureless cysts which surround the pupa forms of *Distomata* imbedded in the body of snails, or to those similarly structureless cysts which enclose the encysted *Tetrarhynchi*, and which Van Beneden saw in course of formation by a process of exudation, around the Scolex form of those worms. The innermost layer of this, which, for distinction's sake, I will call the *Ectocyst*, is whiter and softer than the others, and appears to be in course of formation.

The inner portion of the wall of the *Echinococcus*-cyst is closely

* I beg here to express my obligations to the Secretary of the Zoological Society, without whose kind recollection of a wish to examine fresh Entozoa, which I had expressed, I should not have had the opportunity of making the observations contained in the present paper.

adherent to the last-described layer of the ectocyst, but may, with great care, be separated from it, when it is at once evident that there is no organic connexion between the two; this layer may be very conveniently termed the *endocyst*—it is the only active living part of the whole wall of the cyst, and represents the proper body-wall of the animal. It is very pale and delicate, and not more than $\frac{1}{2000}$th of an inch thick. It is composed of very delicate cells $\frac{1}{2000}$—$\frac{1}{5000}$th of an inch in diameter, without obvious nuclei, but often containing clear, strongly refracting corpuscles, generally a single one only, in a cell. These corpuscles appear to be solid, but by the action of dilute acetic acid, the interior generally clears up very rapidly, and a hollow vesicle is left of the same size as the original corpuscle. *No gas is developed during this process*, and sometimes the corpuscles are not acted upon at all by the acid, appearing then to be of a fatty nature. A strong solution of caustic ammonia produces a concentrically laminated or fissured appearance in them. Under pressure, and with commencing putrefaction, a number of them sometimes flow together into an irregular or rounded mass.

The inner surface of the endocyst is sometimes irregularly papillated like a glandular epithelium in consequence of the prominence of separate cells, or its surface presents an even contour, from the presence of a structureless membrane, which varies in thickness, and seems to represent the inner portion of the blastema, elsewhere slightly granular, in which the cells are imbedded.

Solitary hooks are scattered over the inner surface of the endocyst. I thought at first that they had fallen from the *Echinococci*; but it is with some difficulty that, even by the aid of pressure, the hooks can be so detached from them; and furthermore the hooks in question had generally the appearance of those forms found in the younger *Echinococci*, from which there is still greater difficulty in detaching them. I conclude then that these hooks are developed where they are found, and that they represent a sort of attempt to develope an *Echinococcus* which has gone no further. Within the substance of the endocyst one may see here and there traces of clear delicate vessels, such as those which will be described in the secondary cysts; but probably in consequence of the granular nature of the membrane, they are rarely visible.

In describing the development of the *Echinococci*, it will be necessary to return to this endocyst—at present I pass to the contents of the cyst. This is a clear, colourless, serous liquid, in which two kinds of bodies are found floating, *a*. *Echinococci*, and *b*. secondary cysts.

a. *Echinococci*. To avoid circumlocution, I restrict this term in the present place to what are commonly called the *Echinococcus*-heads.

The *Echinococci* are minute, oval bodies, varying, according to the state of contraction in which they are found, from $\frac{1}{200}$—$\frac{1}{80}$th of an inch in their long diameter.

When fully extended, the *Echinococci* are divided by a constriction into two portions; an anterior somewhat conical part, and a posterior

oval portion, notched at the extremity: attached to the posterior section, and, as it were, sunk in the notch, there is a small appendage of variable form, which usually appears to be clear and somewhat oval, or pyriform, with an irregular ragged extremity.

The body of the *Echinococcus* consists of a very clear transparent substance, slightly granular or dotted internally, and limited externally by a well-marked structureless layer. Forming a circle round the conical anterior extremity there are from twenty to thirty strong hooks, which sometimes appeared to be in a single, sometimes in a double row. In the latter case the hooks of the upper row alternated with those of the lower. A delicate longitudinal striation, as if produced by muscular fibres, extends from the circlet of hooks through the anterior portion, becoming spread out and lost in the posterior.

The hooks were about $\frac{1}{700}$th of an inch in diameter. Their outer half was formed by a strong, curved, conical claw, the inner half by a somewhat crooked process with a blunt end. From the posterior surface of the junction of these two portions a strong rounded spur passed backwards and gave the hook additional firmness in its place. The hook contained a cavity, a process of which passed into each of its portions. Altogether it was not unlike the thickened liber-cell of a plant.

Behind the circlet of hooks, the shape of a transverse section of the body is quadrilateral, and at each of the four corners a large rounded disc with a more or less flat surface is to be seen,—the sucker. In structure, when unaltered, the suckers appear to be homogeneous, with granules and two or three of the peculiar corpuscles to be described immediately, imbedded in their substance. Under the action of acetic acid, however, a radiated fibrillation frequently became visible.

Scattered through the substance of the *Echinococcus*, and giving it a very peculiar dotted appearance under a low power, a number of oval, strongly refracting corpuscles may be observed. They are very uniform in size, and have a long diameter of about $\frac{1}{2500}$th of an inch. They are what have been called the *calcareous corpuscles* of the *Echinococcus*;—inasmuch as in the *Cysticerci* and other cystic worms they have been observed to be converted into carbonate of lime; but I believe that this is entirely a result of that peculiar degeneration to which the cystic Entozoa are so liable, and that, in the young and normal adult state, these peculiar corpuscles (which are found in all the *Cestoidea* and *Cystica*) are never calcareous, but are composed of an albuminous substance.

The mistake has arisen, I think, from two causes. In the first place, because in old cystic worms these corpuscles *are* frequently converted into a calcareous substance, although they retain their transparency and strongly refracting powers; and secondly, because when acid is added to a number of *Echinococci*, gas is very commonly developed from calcareous substances contained either in them or in the fluid in which they swim; at the same time the action of the acid rapidly causes the corpuscles to become clear vesicles, so that nothing seems more natural than to connect the one circumstance with the other.

Having paid great attention to the process, however, I can decidedly affirm—

1. That acetic acid dissolves out the contents of the corpuscles in young and fresh *Echinococci*, without the least evolution of gas from them; and that the same assertion holds good of the corresponding corpuscles contained in the spirit specimens of *Tænia* and *Bothriocephalus* which I have examined.

2. That caustic ammonia produces little cavities and sometimes a concentric lamination in these bodies.

And, 3rdly, that in a spirit specimen of an *Echinococcus* from the Panther (which Dr. Hyde Salter kindly lent me), the corpuscles appeared vesicular without the action of any reagent.

It may be said then, that the peculiar strongly refracting corpuscles of the cestoid and cystic Entozoa usually contain an albuminous substance, and sometimes a fatty matter, but that this is very liable to become replaced by a calcareous substance.

Homologically, I think they are identical with the peculiar, elongated, strongly refracting, solid bodies, contained in the skin of both the *Dendrocœle* and *Rhabdocœle Turbellaria*, which in some marine *Planaria*-larvæ, according to Prof. Johannes Müller, are developed into true thread cells, similar to those of the hydroid Polypes. The thread cell of the latter is equally developed as a secondary deposit within a vesicle (nucleus?) contained in the cells of the body; the only difference would be, that whereas in the Polype the succeeding internal deposit takes place in the form of a spiral thread, in the cestoid or cystic Entozoon it takes place as a succession of simple layers, until the vesicle is full.

Aware of the discoveries that have been lately made by Siebold, Van Beneden and Guido Wagner, as to the extent to which the water vascular system is developed in the Cestoid Entozoa; and unacquainted with what had been observed by Dr. Lebert* (vide *infra*), I particularly endeavoured to detect, in the quite fresh *Echinococci*, some evidence of its existence, and I was so far successful, that I could very readily observe in several specimens (examined on the first day) a number of the peculiar flickering cilia so characteristic of this system of vessels wherever it exists. In spite of all my endeavours, however, I could trace nothing of the vessels themselves, in which, by analogy, one has every reason to believe the cilia are contained†. In one *Echinococcus* I observed six of these long flickering cilia; they were so distinct as to be perfectly measurable, their length being about $\frac{1}{3500}$th of an inch. They were excessively delicate, but broader at the fixed than at the free end, and they completely resembled the corresponding organs in the *Rotifera*‡, *Naiadæ*, &c.

* Prof. Virchow, and the colleagues before whom he laid his observations upon the occurrence of cilia in the pedicle of *Echinococcus* (vide *infra*), appear equally to have overlooked Dr. Lebert's excellent paper, although it is contained in Müller's Archiv for 1843.

† In the *Planaria torva* I have similarly observed the cilia but not the vessels.

‡ See the essay by the author on "*Lacinularia socialis*, &c. &c." in the Quarterly Journal of Microscopical Science, No. 1, 1852.

Professor Owen has stated (article *Entozoa*, Todd's Cyclopædia, 1839) that the *Echinococci* (from the Pig) which he examined, moved "freely by means of superficial vibratile cilia," p. 118. There were certainly no such cilia upon the *Echinococci* of the Zebra.

The movements of the *Echinococci*, so far as I witnessed them, were confined to slow, undulatory, peristaltic contractions. I found numbers in every stage of contraction, but I could not observe any actually performing the process. The head with the hooks is drawn in first, as one meets with many forms in which the suckers only protrude at the extremity, like four knobs. The suckers then follow and are turned completely in, so that their proper outer surfaces look towards one another, the coronet of hooks lying beneath them. In this state, which has been so often described, the animal has not more than half its previous length, and takes on a great variety of forms, oval, rounded, heart-shaped, &c.

b. The secondary cysts.—When the fluid contained within one of the large *Echinococcus*-cysts is emptied into a glass vessel, it is at first turbid with minute white bodies, but these rapidly subside and form a sediment at the bottom of the vessel. These white bodies vary in size from $\frac{1}{80}$th of an inch in diameter downwards to $\frac{1}{100}$th. They are the secondary cysts.

Under the microscope these bodies are seen to be delicate spheroidal sacs, containing *Echinococci*. The largest examined had at least thirty of these in its interior. It consisted of a very transparent structureless membrane, apparently lined by a delicate granular film, which was most distinct near the pedicles of the contained *Echinococci*. These *Echinococci* in fact were not free like those contained in the primary cyst, which I have previously described, but each was attached by a delicate cord, more or less resembling the "appendage" of the free *Echinococcus*, to the inner wall of the secondary cyst, and radiated thence inwards. These *Echinococci* resembled in all respects those previously described, except that I could observe no ciliary motion in them*; they were in all conditions of protraction or retraction, and exhibited the ordinary movements. None were ever found free in a secondary cyst, and the members of each cyst, as well as those in different cysts, were as nearly as may be of the same size and degree of perfection.

The space left between them in the interior of the secondary cysts was sometimes filled with a clear fluid, and at others more or less obscured by granules. In none of those observed by me was there any trace of the peculiar mode of development of the contained *Echinococci* from the granular contents of the secondary cysts described by Von Siebold (vide *infra*).

The membrane of these cysts was traversed by a meshwork of fine clear delicate vessels, with distinct walls and about $\frac{1}{10,000}$th to $\frac{1}{16,000}$th of an inch in diameter. These were not folds, as their lumen could be

* This may well arise from my not having examined them till the 28th. Lebert appears to have found the observation of the cilia to be favoured by the interposed membrane of the secondary cyst (vide *infra*).

clearly seen at the edge of a cyst. They terminated in a somewhat wide space at the base of the pedicle of each contained *Echinococcus*, and in one instance I traced a vessel for some distance into this pedicle. There were no cilia nor granules contained in these vessels, but they precisely resemble those canals of which traces were seen in the Endocyst, and their development will, I think, show that they are identical with them.

I may anticipate so far as to say that I believe that these vessels represent the water vascular system of the parent-cyst.

When such a sac as this is burst the *Echinococci* become everted, and the secondary cyst turns itself inside out, so that the *Echinococci* appear to be seated like Polypes upon a central stem. This curious peculiarity has led to much misconception as to the mode of their attachment *within* the cyst. Von Siebold, however, pointed out the true nature of this process as far back as 1837* (vide *infra*).

The smallest free secondary cysts varied in size, as I have said, down to $\frac{1}{100}$th of an inch, when they contained only four *Echinococci*. These, however, were quite as large as those in the largest secondary cysts.

The structure of the middle-sized and small vesicles was in most respects the same as that of the large ones, but there was this difference, that they possessed, attached to their outer surface, by pedicles, a variable number of oval bodies of the same average size as the *Echinococci* or less, but presenting a yellow wrinkled appearance, containing very few corpuscles, often none, and either exhibiting no trace of the circlet of hooks, or offering only a few, dark irregular and withered-looking ones. It was impossible to confound these *external* bodies with accidentally everted *internal* heads, the appearance of the two being markedly different.

I cannot help thinking that these withered *Echinococci*—for that, as will be seen presently, is what they really are—are what Mr. Erasmus Wilson has figured as developing forms (*loc. cit.*).

Development.—We have found free *Echinococci* and free secondary cysts contained in the fluid of the primary cyst: how do they come there? To answer this question we must return to the endocyst. I found adherent to, and growing from it, *a.* fixed *Echinococci*, and *b.* fixed secondary cysts.

a. Fixed Echinococci.—These, in various stages of development, are scattered all over the inner surface of the endocyst, as in the diagrams E. and F. Plate XI.

Elongated elevations of the endocyst are first seen: within these the circlet of hooks and then the corpuscles make their appearance: the elevation becomes a papilla, and the papilla, gradually constricting itself at the base, becomes the oval *Echinococcus*, attached by a narrow pedicle. In this state the slightest touch is sufficient to separate the pedicle from the endocyst, and then the *Echinococcus* is

* The *Echinococci* are figured in this everted state by Chemnitz (quoted by Siebold, art. *Parasiten*, Wagner's Encyclopædia, &c.), by Erasmus Wilson (Medico-Chir. Transactions, 1845), and by Busk (Microscopical Transactions, 1846).

set free. The pedicle contracts upon itself so as to have a rounded form, but it very often betrays its previous adherence by the ragged fragments of the endocyst, which it carries with it.

Whether this is properly a normal process in the *Echinococcus* it is difficult to say, but as Dr. Guido Wagner and Van Beneden have shown, it occurs normally in the *Tetrarhynchidæ*, and it exactly resembles that detachment of the "tail" from the *Cercaria*, which takes place in the *Distomata*.

As little is it known whether the *Echinococci* undergo any further development. The suggestion first made by Delle Chiaje, that they may dilate into cysts and develope young *Echinococci* within themselves, appears to me highly improbable; and it is an hypothesis which is not needed to account for the secondary cysts.

b. Fixed Secondary Cysts.—The development of these indeed takes place in such a manner as to preserve the homological relations of the *Echinococci* to the exterior of the parent. The secondary cysts, in fact, are thus formed: *Echinococci* are developed not only from the inner surface of the endocyst, but from its outer surface. Their growth is probably accompanied by that of the endocyst itself, which thus becomes raised up from the ectocyst and projects into the general cavity. Of course any internal *Echinococci* which happen to be attached to this part of the endocyst are raised up with it: they may be fewer or more according to circumstances. The neck of attachment of the secondary cysts gradually narrows, and at last the secondary cyst, whose size depends entirely upon the number of *Echinococci* developed under the endocyst at one spot, is detached and falls into the cavity. So long as the secondary cyst remains attached, its external *Echinococci* have the normal clear appearance, and are in full health; but when once it is separated, they appear rapidly to wither away and become yellow, losing their hooks and their corpuscles, and eventually disappearing. The original point of attachment of the sac remains as an obtuse cicatrix.

Von Siebold, who has beautifully described the development of the secondary cysts, has, I think (vide *infra*), mistaken the *one* mode of development of the *Echinococci* outside the endocyst for the *only* mode. He appears to have seen the endocyst, when he describes the "delicate membrane in which the young *Echinococcus*-heads are enclosed," and to *assume* merely, that this membrane bursts and sets the *Echinococcus* free upon the inner surface of the parent cyst. Understanding the mode of development to be as stated above, it is easy to comprehend how it is, that the *Echinococci* are so nearly at the same stage of development in all the secondary cysts; and that this stage has no relation to the size of the cysts. The existence of the external *Echinococci* upon the secondary vesicles in this way also, becomes not only intelligible, but almost necessary.

II. The theory which I have to offer of the nature of the *Echinococcus*, is based upon three facts which are now well established. 1st. That young Cestoid Worms, which, from some cause or other, have passed into any other part of the organism of the animal upon which they are parasitic, than the intestine, become abnormally

dilated, at their posterior extremity; and the anterior end may be retracted into the sac thus formed, which then invests it like a double serous sac—a structureless investment may be excreted round this encysted worm or it may not. Such an altered Cestoid Worm as this is called a *Cysticercus*.

2ndly. A dilated Cestoid worm, such as has been just described, may develope new "heads" with suckers and hooks all over its outer surface, never developing any upon its inner surface. Such a Cestoid worm is the *Cœnurus cerebralis*.

3rdly. The Cestoid worms all possess the power of gemmation (or it may be called fission) in their unaltered state: and Bendz (Isis, 1844) has distinctly shown that the vesicular extremity of the *Cysticercus* gemmates. Processes are formed and thrown off, and these develope appropriate heads and hooks, becoming complete *Cysticerci*.

Bearing these facts in mind, it is I think very easy to account for the *Echinococcus*-vesicles. The surfaces which produce the *Echinococci* must be *both external*; the *Echinococcus*-cyst therefore does not answer to the simple cyst of the *Cœnurus*, or of the protruded *Cysticercus*; but to the double cyst of the retracted *Cysticercus*, the upper half of whose proper outer surface forms the inner wall of the cyst in the retracted state (see Diag. D. Pl. XI.).

Suppose the cyst, thus formed, to dilate and to develope a multitude of heads upon this upper half of the outer surface, after the analogy of *Cœnurus*; then the two walls being pressed together into one, it will appear like a simple cyst covered with heads internally (Diag. E.).

If, however, at the same time, in complete correspondence with *Cœnurus*, heads have been developed over the whole outer surface, we have the primary *Echinococcus endocyst* (Diag. F.).

Now the cyst may grow out at a particular point, and so form a bud, which is cast off externally. This takes place in the *Echinococcus* of Oxen. But if it have surrounded itself with a dense cyst, analogous to that of the encysted *Tetrarhynchidæ*, such external budding cannot take place; and if the local growth takes place at all, it will produce a projection internally, and the internal fixed secondary cysts will be produced. These, narrowing at the neck and detaching themselves, become the free secondary cysts, as was shown above.

The *Echinococcus* then is a species of *Tænia* which has become dilated and encysted; which has subsequently produced heads all over its external surface, and finally, budding, casts off its vesicular processes internally, because it has no exit for them externally.

Echinococcus is thus the most complex form of that change which young Cestoid Worms are liable to undergo if they wander from their proper nidus; the combination of hooks with suckers refers it to the genus *Tænia*, to which *Cœnurus* and *Cysticercus* may by similar reasoning be shown to belong; and, therefore, like these two latter genera, it must, as a genus, be abolished. It is probable however that *Cysticercus*, *Cœnurus* and *Echinococcus* are modifications of distinct species, or groups of species, of the genus *Tænia*; and are not mere varieties of one species produced by difference of locality. They are all three found in the brain, for instance.

As to the genus *Acephalocystis*, there is good reason for believing, that all genuine specimens of it are *Echinococcus*-cysts which have either not developed heads, or in which they have been overlooked.

The converse of the anatomical evidence as to the identity of *Echinococcus* with a modified *Tænia*, has just been supplied by some very beautiful researches of Von Siebold's, published in the Annales des Sciences for 1852 (or Annals of Natural History, December 1852). Von Siebold gave to young puppies spoonfuls of *Echinococcus*-cysts in milk. Upon opening them after a short time, he found *innumerable Tæniæ attached all over the surface of the intestine*. The cysts had been digested, but the living *Echinococci* had resisted the action of the stomach, and, freed from their imprisonment, had begun to develope joints. Growth had not gone on sufficiently to enable the learned Professor of Breslau to determine the species. He promises, however, a continuation of his researches; and it is to be hoped that we may soon have a complete clearing up of the difficulties with which helminthologists have so long been puzzled, from his able pen*.

III. The literature of *Echinococcus* exhibits a singular instance of the manner in which naturalists delay their own progress, by not attending to what has been done by their predecessors. Goeze wrote in 1782, and effectually demonstrated the cestoid relations of the *Echinococci*, as may be seen by the following extracts from his beautiful work (Versuch einer Naturgeschichte der Eingeweidewürmer); nay, before his time, Pallas had on very good grounds conjectured the same thing, and yet half a century afterwards we find this all forgotten, and speculation rife as to the nature of the *Echinococci*.

Goeze thus describes the *Echinococcus*-vesicles (*op. cit.* p. 258 *et seq.*):—

"C. The small social granular Bladder tape-worm (Blasen-bandwurm): *Tænia visceralis socialis granulosa*.

"This is as it were an intermediate form between the great globular Bladder tape-worm (*Cysticercus*), and the many-headed worm found in the brain of staggering Sheep.

"I had already read what Pallas supposes on this subject in the 'Neue Nordische Beyträge,' i. p. 85, when, by a lucky discovery, I made the whole matter out.

"Upon the 1st of Nov. 1781, I met with an excessively distorted Sheep's liver, which was so beset and penetrated by large and small watery vesicles,—the former as large as hens'-eggs, the latter as hazel-nuts,—that, externally, one could discern hardly anything of the substance of the liver.

"The animal itself was almost perfectly healthy. In its total size, this monstrous liver was about equal in breadth to the two hands; and its length was about half an ell: the weight however was four pounds. I was obliged to divide it into two portions in order to be able to get it into a large jar (3 inches, glass) with spirit. When I pricked one of the vesicles with a needle, the water spirted out, as out of a fountain. I observed, however, that the distended vesicles con-

* A full account of Siebold's investigations has, in fact, appeared in Siebold and Kölliker's 'Zeitschrift' for 1853, under the title, "Ueber die Verwandlung der Echinococcus-brut in Tænien."—T. H., April 1854.

tained nothing beyond a mere lymph and possessed no special internal vesicle. In separating the one portion of the liver I could not avoid damaging some of the vesicles contained in its interior. Out of these tolerably hard leathery external vesicles, fell bluish, callous (kallöse), internal vesicles, which were still closed. In their substance indeed they were somewhat softer than the outer vesicle; but still far more cartilaginous than the vesicles of the globular, many-headed bladder-worms. On opening these there was found internally in different places a greyish granular matter like the smallest fish roe, which was united to a very delicate mucous membrane, [which] in water however immediately disappeared, so that the granules swam about by themselves. In a vesicle as large as a dove's egg there were thousands, so small that they could hardly be distinguished by the naked eye. Under No. 4. Tub. A of my microscope I could already perceive the organization of these corpuscles. Their form varied greatly; sometimes heart-shaped with an indent above and a dark line; sometimes pitcher-shaped, with two round knobs above, at each side one; sometimes like a horse-shoe with a short dark middle line; sometimes like a rounded handle, with an indent above and with two knobs laterally, and anteriorly rounded off with a dark circlet. When I used No. 1. Tub. A, I saw clearly that they were true tape-worms. The body flat with dark dots; anteriorly four suckers, and on the obtusely rounded proboscis, the double circlet of excessively small hooks; behind, however, in each there was a small excavated indentation like an anus. The others were contracted in quite peculiar forms, and the dark median streak was the hook circlet. Under the compressor, the four suckers, the circlet of hooks and the points become much clearer. In these worms I have observed a circumstance which I have perceived in no other kind of bladder-worm; namely that on pressure the delicate hooks are detached and float about freely.

"This kind of bladder-worm is distinguished then from that inhabiting the brain of staggering sheep by the following circumstances:—

"1. That the vesicles with the granular matter or with many thousand infinitely small worms, are covered by a strong leathery external vesicle in which they lie free.

"2. That their roe-like material swims about in the inner vesicle in a clear lymph, and the single worms are only united together by a delicate mucous membrane, but are not as in those, essentially adherent to the bladder, and not even to their [own] membrane.

"3. That each of these granules or worms is several hundred times smaller than one of the white corpuscles or worms in the central bladder of the staggering sheep.

"This is then the same, but now explained phænomenon, which the acute Pallas has already observed; but has left without elucidation.

"In the 'Stralsund Magazine,' 1. St. p. 81, he has already directed the attention of observers to these points:

"'Whoso will consider the above description of the true bladder-worm, will not perhaps with M. de Haen deny to worms all participation in the origin of watery tumours and of Hydatids, at least it seems to me very probable that the unattached (unangewachsene) watery bladders seen by many observers in the human body—most

frequently in abnormal cavities in the liver—are caused by a worm similar to, if not identical with, our bladder worm, I say from a worm *probably resembling our* bladder-worm; for we find in the liver and lungs of Oxen and Sheep another wonderful kind of watery bladder, which seems to arise from nothing but some kind of animal germ; but however is widely different from our bladder-worm, and cannot have arisen from it.'"

Pallas, after describing some of the Hydatids, goes on to say:

"The water-bladder itself consists of a white, hardish, quite homogeneous membrane, which becomes thinner towards the caudal extremity; wherever it is lacerated it folds back, and may be best compared with a section (as thin as paper) of a boiled cartilage of a young animal. Within, this external strong membrane is lined by a delicate structure or membrane, which is very easily separated from it, and is beset with a great number of small, white, commonly round, or oval, corpuscles. The corpuscles consist, as the microscope shows, of longish globules united together, whose substance appears to be dotted."

Subsequently (p. 261) Goeze quotes from the 'Nordische Beyträge,' 1. St. p. 83, thus:

"It is probable that the unattached hydatids which are at times observed in the human body (are), either of the same kind as the proper bladder-tape worm, or are the same as those singular watery bladders, which I have observed and described in the liver and lungs of diseased Calves and Sheep, and which are most certainly also to be ascribed to a living creature, and are not indistinctly organized (at least if we consider the inner membrane strewed over with granular globules).

"On reading through Leake's treatise upon the 'Staggers in the Sheep,' p. 85, it seems very probable to me that the bladders in the brain are more similar to those which I have described in the lung and liver in Sheep and Calves, than to the bladder-worm which Tyson and Hartman have described before me (our globular one); nay perhaps, that they even constitute one genus with the former. The small worm provided with a circlet of hooks and four suckers, in these vesicles, might be a development of the globules observed by me.

"I have at present no opportunity of examining these vesicles in the fresh state. Perhaps on applying a stronger magnifying power the granules might exhibit more organization.

"Consequently, Pallas did not at that time know what to make out of the granules of these vesicles. The peculiar organization of these he did not himself see, as I have now discovered, described and figured it. To whom then belongs the first and true discovery of the nature of the granules in the internal membranes of the singular Hydatids of the livers and lungs of Calves and Sheep?

"But I wish that I could throw more light upon and explain the mode of origin of these vesicles, and upon the œconomy of the many thousand single worms socially united in a single bladder. Do they grow? do they disperse themselves? does each build its own dwelling? or where do they remain? shall our successors learn nothing on these matters?"

Goeze's figures are very good.

The commonly received view of the relation between the cysts and their *Echinococci* appears to have been first advanced by Delle Chiaje in his *Elmintografia Umana*, p. 30*.

"The said worms, oval, narrowed at the two extremities and enlarged in the middle, are scattered irregularly over the interior of the vesicle. The extremity of the head is garnished with a crown of hooks deprived of suckers. In proportion as they enlarge, these little microscopical bodies take on, little by little, a spherical form, the hooks become detached, and new *Echinococci* are produced in such little bodies, which have transformed themselves into Hydatids. The new worms are the children (figliuolini) of the primitive Hydatid, which was a similar microscopic body. They have a proper vitality, different from that of the vesicle which contains them."

Müller, 'Jahresbericht,' 1836, describes the *Echinococcus*-cysts and their contents found in the urine of a young man labouring under renal disease.

The cysts had a laminated outer coat; some contained *Echinococci* and some none, but in other respects they were completely alike. The *Echinococci* exactly resembled the ordinary figures.

"In a few of the free ones, a trace of a membranous cord, looking as if it had been torn off, appeared at the posterior end of the body; as if the worms had at an earlier period been fixed."

Müller could not make out whether the *Echinococci* were fixed to the interior of the secondary vesicle or not.

Tschudi, 'Die Blasenwürmer, 1837,' observed the retrograding yellow *Echinococci*, which he assumes to be returning to the vesicular form. He considers that the "corpuscles" are ova, and that by their development in the interior of one of these retrograded *Echinococci*, the secondary cysts are formed.

Gluge, 'Annales des Sciences Naturelles, 1837,' describes the corpuscles of the *Echinococci* very carefully and minutely. He was the first to notice the peculiar structure of the endocyst. He says, "I have constantly seen in it a kind of arborization very similar to the formation in fibrinous exudations during the first stage of inflammation. We see these transparent bodies with slightly irregular contours resembling empty blood-vessels and ramifying like them. I do not know whether these are true vessels, I merely draw attention to the fact."

In the same year (1837) the second edition of Burdach's 'Physiologie' appeared. It contains an admirable chapter by Von Siebold, upon the development of the Entozoa. Burdach's work is so little known, and so inaccessible in this country, that I think it worth while to subjoin the whole of what Von Siebold says upon this subject:—

"In the development of the *Echinococci* also, much has remained obscure. We must in them always distinguish two things; the parent vesicle, and the proper *Echinococci* enclosed within this. The maternal vesicle is covered internally by an excessively delicate epithelium, in which are contained corpuscles similar, though here

* *Compendio di Elmintografia Umana.* Napoli 1825. Compilato da Stephano Delle Chiaje.

generally elongated, to those which we have found in the neck of *Cœnurus*. In the fluid which the maternal vesicle encloses, we meet with a few *Echinococci*, which when they have everted their coronet of hooks and their suckers, allow nothing to be perceived in their interior but a few scattered glassy corpuscles. These *Echinococci* evidently arise from the inner surface of the parent vesicle. My own observations hereupon have been made upon *E. hominis*, *E. veterinorum*, and a new species which, since the number of its suckers varies very much, I will call *E. variabilis*. On examining the inner surface of the parent vesicle we see little vesicles attached here and there, which contain a finely granular substance; out of this mass the *Echinococci* proceed (hervorkeimen), sometimes only one, sometimes two, six, seven or more. A portion of the granular mass becomes, in fact, sharply marked off, forms a small roundish body, which, however, by one of its ends, still clearly passes into the rest of the substance; the rounded body gradually takes on a pea shape, the constricted portion elongates, and the body, which has now assumed a more oval form, is connected only by a delicate viscid thread with the mass from which it sprang; we soon now observe in the interior of the body the circlet of hooks and the glassy corpuscles. The *Echinococcus*-head thus far developed now begins to move—everting and retracting its suckers and hooks; the whole body being at the same time sometimes elongated, sometimes contracted. The development of the *Echinococci* having proceeded to this stage, the delicate membrane in which they are enclosed bursts. The young *Echinococci* do not immediately fall out, for they are all connected to the inner surface of the membrane, which until now has enclosed them, by means of a delicate cord or process of the latter, which penetrates at the posterior extremity of the *Echinococcus*, through a pit, into the interior of the body of the *Echinococcus*. The pit looks almost like a sphincter, holding just that cord of the membrane; only after an interval do the cords and the bodies of the *Echinococci* become separated. The mode of connection of these cords with the bodies of the *Echinococci*, and their separation from them, reminds one completely of the relation which the bodies and tails of the *Cercariæ* have to one another. The membranous covering of the young *Echinococci* wrinkles up immediately when it is torn. The *Echinococci* become everted, and so form a rounded heap, in the middle of which the collapsed investment lies hidden, the *Echinococci* being attached to it like the polypes upon a polypidom.

"Such masses of *Echinococci* either remain for a long time hanging to the inner surface of the parent vesicle, or they become detached from it before the single *Echinococci* have separated from the wrinkled membrane. The granular mass contained in the vesicles is probably comparable with nothing else than with a yelk mass, which supplies the heads with the substance necessary for their development through those fine cords. For the rest, I will not undertake to decide whether all those larger and smaller vesicles, which contain *Echinococcus*-heads and float about free among fully-developed *Echinococcus*-heads in the cavity of the parent vesicle, are de-

tached from the wall of the latter, or whether some few of them do not arise from the free *Echinococcus*-heads themselves, which have developed *Echinococcus*-germs in their interior, and afterwards become distended into vesicles by them; I was often surprised, in fact, to find upon free vesicles containing *Echinococcus*-heads, hooks attached, perhaps remnants of the destroyed circlet of hooks. In such vesicles of *E. variabilis*, in fact, I believe I could trace remains of the suckers. With greater difficulty can we understand the mode of origin and propagation of the maternal vesicle of the *Echinococci*. Since in *Echinococcus hominis* we often find smaller hydatids enclosed within larger ones, we must believe that the external hydatid is the parent in which the others have been subsequently produced. In what manner, however, this enclosure has taken place, I must leave as much unsolved as the origin of the parent vesicle itself."

The next step was made by Dr. Lebert, in his excellent paper (unfortunately without figures), "Einige Bemerkungen über Blasenwürmer," in Müller's Archiv for 1843. From this I make the following extracts:—

"In the most, even freshly examined hydatids, the animals no longer move. Yet not unfrequently, if many vesicles be examined, living groups may be met with. The movement of the animal, while still in the maternal vesicle, consists partly in turning upon its axis, partly in a wavy contraction, comparable to a peristaltic movement. In the interior of these yet living and moving animals I have perceived ciliary motion very clearly. It appeared in the whole interior of the animal, and I could observe it for hours together. At first I could with difficulty distinguish the single vibrating cilia; yet, partly after partial evaporation of the fluid in which the animals were contained, partly by modifying the light with a very fine perpendicular diaphragm, I could succeed in seeing the cilia themselves, which are slightly curved and somewhat hook-like, and hardly more than $\frac{1}{800}$ mm. in breadth. I have seen the single cilia with especial distinctness towards the margin of the animal; commonly, however, they are indistinct, on account of the contemporaneous vibration of a certain number of cilia, which resemble in their motion a field of corn agitated by the wind. The observation of this ciliary motion was perhaps rendered more easy by the circumstance, that I observed the animals still adherent to the finely granular membrane which forms the parent vesicle, and which, in all probability, favourably modified the light."

"As to what concerns the development of the vesicles themselves, it seems to go on in the following manner:—upon the inner wall of a cyst which contains *Echinococcus*-cysts, secondary cysts are formed, which, after they have attained a certain grade of development, become detached from the inner wall of the larger cyst, and fall freely into their cavities, but still show the remains of their attachment in a slightly pointed place: on the inner surface of these secondary vesicles tertiary ones are now formed in the same manner, and so on. The hydatid sacs then arise by a kind of endogenous formation simi-

lar to that which Prof. Müller has already so beautifully described in the development of a peculiar kind of hydatid tumours.

In his Article "Parasiten" (Wagner's Handwörterbuch d. Physiologie, bd. 2, 1844), Von Siebold, after recapitulating his view of the development of the *Echinococci* contained in Burdach's Physiologie, makes the following highly suggestive remarks:—

"Clearly as we can trace the development of the young of the *Echinococcus*, we understand very little of the mode in which the pill-box (eingeschächtelt) aggregations are produced. The multiplication of the vesicles certainly does not take place by division, nor by the formation of buds upon the outer surface of the parent cyst, as some have supposed. The hypothesis remains, that the young *Echinococci* cast off their circlet of hooks, become distended, lose their suckers, and so change into little *Echinococcus*-vesicles, in which a new brood then becomes developed. I must indeed confess that I have not directly observed this process. In any case, the young *Echinococcus* must be in a fit state to wander; and if it should be made out that new *Echinococcus*-vesicles proceed from them in the interior of the parent vesicles, we might also justly assume that the young *Echinococci*, wandering into other organs, or even into other persons, may thus lay the foundation for new colonies. Whether, again, there exists a special cestoid worm provided with sexual organs, with which the *Echinococcus*-vesicles stand in the same relation as the *Cercaria*-sacs do with certain *Trematoda*, time will show. If it be so, the young *Echinococci* must change, having become separated from their pedicle, not into *Echinococcus*-vesicles, but by the elongation of the body into *Tæniæ*."

Finally, in the 'Verhandlungen der Physikalisch-Medicinischen Gesellschaft zu Würzburg' for 1850, (to which my attention was drawn by my friend Mr. Busk,) I find the following notice:—"Herr Virchow described the ciliary movement which he had observed in the stem by which the young *Echinococci hominis* of Man are attached to the maternal vesicle,—a new observation for this genus."

I have here endeavoured to notice all those Memoirs which, at the time of their publication, made a definite addition to what was already known upon the structure of *Echinococcus*. The literature of the subject is somewhat voluminous, and hence the necessity of this limitation, and the consequent absence of any account of the valuable memoirs of Goodsir, Curling, Busk, and Erasmus Wilson, all of whom had been anticipated by the continental observers.

EXPLANATION OF PLATE XI.

Diagrams:—Hypothetical representations of—A. a young *Tænia*; B. a *Cœnurus*; C. a *Cysticercus*; D. the same, encysted; E. a *Cysticercus*, encysted, enlarged, and developing many heads (like *Cœnurus*) from the upper portion of its outer (now inner) surface; F. a similar form, which developes heads from the lower portion of its outer (now wholly outer) surface, and so becomes an *Echinococcus*-cyst.